

THE VALIDITY OF *RAJA RHIZACANTHUS* REGAN AND *RAJA PULLOPUNCTATA* SMITH, BASED ON A STUDY OF THE CLASPER

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(With 8 figures in the text)

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INTRODUCTION

The present classification of South African skates is more or less tentative, for this difficult genus shows great variability in its morphological characters, which vary with age and/or sex in the individuals within the species. This high intraspecific variability probably accounts for the present inclusion of 95–100 species in the genus *Raja*. Several South African species have, as yet, proved to be indistinguishable from European species from the corresponding latitudinal belt in the northern hemisphere (Bigelow & Schroeder, 1953), and it would appear that these pairs represent cases of ‘masked bipolarity’ (Ekman, 1953). But in very few cases have actual comparisons of the specimens from the two regions been made, although Norman (1935) has given some brief references.

Raja alba, Lacépède, from the N.E. Atlantic is reported here under the same name, but it appears to be cosmopolitan in distribution, being recorded from Morocco (Pietschmann, 1906), West Africa (Fowler, 1936) and Angola (da Franca, 1959).

Norman expressed some doubt about the identification of *R. batis* from South Africa but the material he examined included a single stuffed specimen, on which accurate measurements were impossible. This South African species is now thought to be distinct from *R. batis* Linnaeus, and Smith (1964), on the basis of the shape, the presence of a single median spine and the general markings, has reclassified this skate as *R. pullopunctata*, although he points out that only juvenile material was examined.

Raja rhizacanthus Regan, has been thought to be identical with the European thorn-back skate *R. clavata* Linné, but this has been a matter of speculation. Barnard (1925) and Fowler (1940) have included *R. rhizacanthus* as a synonym of *R. clavata*, but Norman regarded the two as distinct species on the basis of spination and the position of the vent. This has been followed by Smith (1961).

It is the purpose of this paper to compare and contrast certain morphological characters, in the hope that the validity of these latter two South African species may be determined with greater certainty.

Since skates show such great variations in external features, a more critical method of examination needs to be employed. Leigh-Sharpe (1920–1926) has pointed out that in the genus *Raja*, individual species can be recognized by the morphological structures of their claspers. He has extended this further and has postulated the existence of pseudogenera (termed *Alpha*-, *Beta*- and *Gamma-raia*, etc.), recognizable by the similar presence or absence of the clasper elements. Ishiyama (1958) has shown that in Japanese rajids, although intraspecific variations in the clasper can be recognized, the 'external and internal structures of the clasper are species specific without exception' (p. 224). On this basis he has also been able to postulate phyletic, generic and inter-specific relationships, and has concluded that 'the characters in the male external organ (claspers) of the Japanese rajids seem to give the most reliable basis for the systematics of this group of fish'. (p. 243.)

Hence it would appear that since the anatomy of the clasper is valid for the purposes of identification, it should also be valid for the purposes of comparison of geographically separated species. However, 'genitalic differences must be evaluated just like other characters' (Mayr *et al.*, 1953, p. 109), and so differences in the external and measurable characters of the specimens must also be taken into account.

THE CLASPERS OR MYXOPTERYGIA

Comprehensive anatomical studies have been carried out on the claspers of European elasmobranchs by Petri (1878), Jungersen (1899) and Huber (1901). Two points of view were held as to the function of the claspers: that they were 'holders' (analogous to hands) was originally postulated, but they were later recognized as organs of intromission. Extensive study on the external anatomy and the function of the clasper in the various elasmobranch groups has been made by Leigh-Sharpe, and further work on the function of the organ has been performed by Friedman (1935).

The nomenclature used in this paper is mainly in accordance with that of Leigh-Sharpe and Ishiyama, together with that of the above-mentioned authors.

THE CLASPER OF *R. RHIZACANTHUS* REGAN

The claspers from seven adult specimens of *R. rhizacanthus*, trawled off Cape Columbine and in False Bay, were examined.

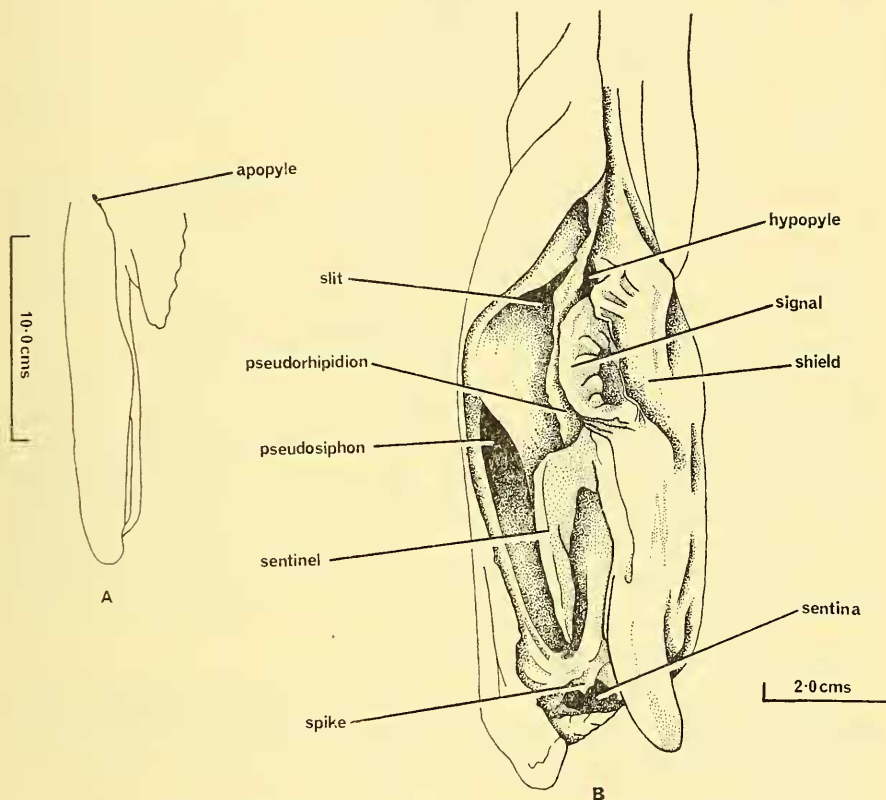


FIG. 1. *Raja rhizacanthus*

A, external view of right clasper from dorsal side; B, lateral view of right clasper, opened to show structural features of glans.

(i) *The external anatomy of the clasper* (fig. 1 A, B)

The clasper of *R. rhizacanthus* is a moderately long, strongly built structure, the outer surface of which is entirely naked. Proximally the clasper is cylindrical, but from about $\frac{1}{3}$ its length from the distal end, it becomes broader and dorso-ventrally flattened, especially on its ventral surface. It tapers gradually towards its distal end and terminates in a broadly rounded, spatulate

tip. The ventral surface is pale and the dorsal surface tones with the general coloration of the body.

The apophyle (fig. 1 A) is situated dorsally, some little distance behind the vent, and the appendix groove, arising from this point, runs across to the outer margin of the organ, and continues along the distal two-thirds of the lateral edge almost to the tip of the clasper. In some cases, due to the skin stretching across the dorsal terminal 1 cartilage, the groove may be seen from the dorsal side. Proximally the groove is bordered on by the two 'scroll-like' dorsal and ventral marginal cartilages, so that the edges of the groove closely approximate to form a tube, running from the apophyle to the hypophyle. Distally, from about half the clasper length, fleshy lips border the groove, and during erection, brought about by the powerful adductor muscles, and by vascular dilation (Friedman), these lips are opened and the structures of the clasper glans protrude (fig. 1 B).

Two pouches are present on the dorsal surface of the concavity of the clasper glans (fig. 1 B), the smaller, more proximal *slit* and the larger, distal *pseudosiphon*. The median *hypophyle* is bordered dorsally by the pseudorhipidion, a plate-like structure employed as a splash-plate for ejaculating spermatozoa and distinguished from the *rhipidion* of Leigh-Sharpe in not being fan-shaped or pitted. Posterior to the hypophyle, and at about the same level as the pseudorhipidion, is a fleshy pad, the *signal*, which is capable of rotation about the longitudinal axis of the clasper. The *sentinel* is strongly developed and in older specimens its knife-like edge is exposed. There is a deep *sentina* situated distally, its inner border raised into a curved spike. The ventral *shield* is narrow and not well developed. The lining of the concavity is naked, *scale* and *spine* being absent.

All these above-mentioned structures are associated with the cartilages of the terminal group.

(ii) *The internal anatomy of the clasper* (figs. 2, 3)

The skeleton of the clasper is a continuation, in the median axis, of the basipterygium of the fin, and is composed of two groups of cartilages, the basal group (including the basipterygium) and the terminal group.

(a) *The basal group* (fig. 2)

Ishiyama has pointed out, that in Japanese rajids, the basal group is not species specific, and, although White (1937) has proved that the number of proximal segments and other cartilages in the basal group tend to vary in large groups of the elasmobranchs, the basal group may only be used in phyletic considerations among the batoid fishes. Examination of the basal group of *R. rhizacanthus* seems to support this view, since the same seven cartilages are present as in the Japanese rajids (see Ishiyama, fig. 7).

The basal group in *R. rhizacanthus* consists of the basipterygium, and b_1 and b_2 cartilages, the Beta-cartilage, and the axial cartilage, which extends

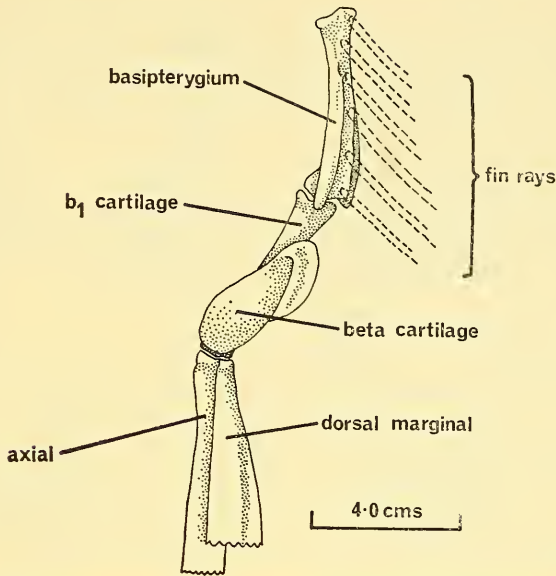


FIG. 2. *Raja rhizacanthus*. Cartilages of the basal group of the clasper.

to the terminal part of the clasper, and is covered by the dorsal and ventral marginal cartilages (fig. 2). The basipterygium is a short, stout structure, to which are attached in a groove on its lateral margin, the last 6 fin rays of the pelvic fin. Distally, the basipterygium is elongated on its dorsal surface to form a protuberance which overlaps the b_1 cartilage. The proximal end of the b_1 cartilage is visible from the dorsal side, but the Beta-cartilage, situated dorsally to the b_1 and b_2 cartilages, completely obscures the b_2 cartilage and the distal end of b_1 . The Beta-cartilage is more or less flat, serving as a region of attachment for the *m. flexor internus*, but is slightly thickened and upraised at its proximal end, forming a shelf.

The distal ends of the b_2 and Beta-cartilage are superimposed so that both of these elements play a part in the joint with the axial and marginal cartilages.

The long axial cartilage is cyclindrical at its proximal end, but it becomes dorso-ventrally flattened distally and assumes a spatulate appearance. It is tightly enclosed by the calcified dorsal and ventral marginal cartilages and is only free at its spatulate tip, although it is visible dorsally. The dorsal marginal cartilage attaches tightly to the axial, starting where the axial is connected to the b_2 /Beta joint, and runs along the outer lateral margin of the axial for about half its length. The dorsal marginal cartilage is somewhat broadly pointed anteriorly but it becomes expanded distally, its outer lateral edge forming the dorsal edge of the 'scrolled' groove of the clasper. The ventral marginal cartilage, unlike the dorsal marginal, starts posteriorly to the axial and is a flat, tongue-like structure. Its outer lateral margin forms the ventral lip of the

'scroll' and medially it is attached to the axial, overlying it distally. The ventral marginal cartilage extends farther down the length of the clasper than the dorsal marginal cartilage. Attached distally to the axial and to the marginal cartilages, are the elements which comprise the terminal group of cartilages.

(b) *The terminal group*

The elements which comprise the terminal group of cartilages are associated with the structures of the glans, and may be divided into three types: ventral terminal, dorsal terminal and accessory cartilages.

1. *Ventral terminal* (figs. 3 A, B, G)

The ventral terminal cartilage is attached to a groove in the distal end of the ventral marginal cartilage. It has a J-like shape, being by far the largest cartilage of the terminal group. It is strongly curved medially, and runs around the axial cartilage, so that it can be seen from the dorsal side. The upright portion of the ventral terminal cartilage is fairly well developed and there is a small shelf on its dorsal side, which is seen as the shield of the clasper glans. Distally, the ventral terminal is thick and somewhat pointed.

2. *Dorsal terminal 1* (figs. 3 C, G)

The dorsal terminal 1 cartilage ('cover-piece' of Jungersen) is situated on the dorsal side of the clasper, partially covering the dorsal terminal 2 cartilage, to which it is attached along the length of its longest margin. It is flatly rounded and curved proximally, so that it is elongated on its outer lateral margin. From this point, there is a shelf, running in a curve along the anterior margin, which serves as a point of insertion for the aponeurosis of the *m. dilatator*, which consequently covers the whole area of the cartilage. Distally, the cartilage is flat and its distal end is attached, together with the dorsal terminal 2 cartilage, to the axial cartilage. The dorsal terminal 1 cartilage is associated with the development of the pseudosiphon.

3. *Dorsal terminal 2* (figs. 3 D, G)

This curved element is inserted between the dorsal terminal 1 and the dorsal marginal/axial cartilages. It is firmly attached to the distal region of the dorsal marginal cartilage, and by means of a ligament (which forms the shelf between the slit and pseudosiphon) it is attached at its distal end to the outer lateral margin of the axial cartilage, at about $\frac{2}{3}$ the length of that cartilage from its anterior end. The dorsal terminal 2 cartilage is strongly curved, and raised along the side of longest curvature, to form a flat surface 'articulating' with the dorsal terminal 1 cartilage. The dorsal terminal 2 cartilage is associated with the slit.

4. *Accessory cartilages 1 and 2* (figs. 3 E, G)

These two cartilages are strongly united and are attached to the distal end of the ventral marginal cartilage. The accessory cartilage 1 is the S-shaped

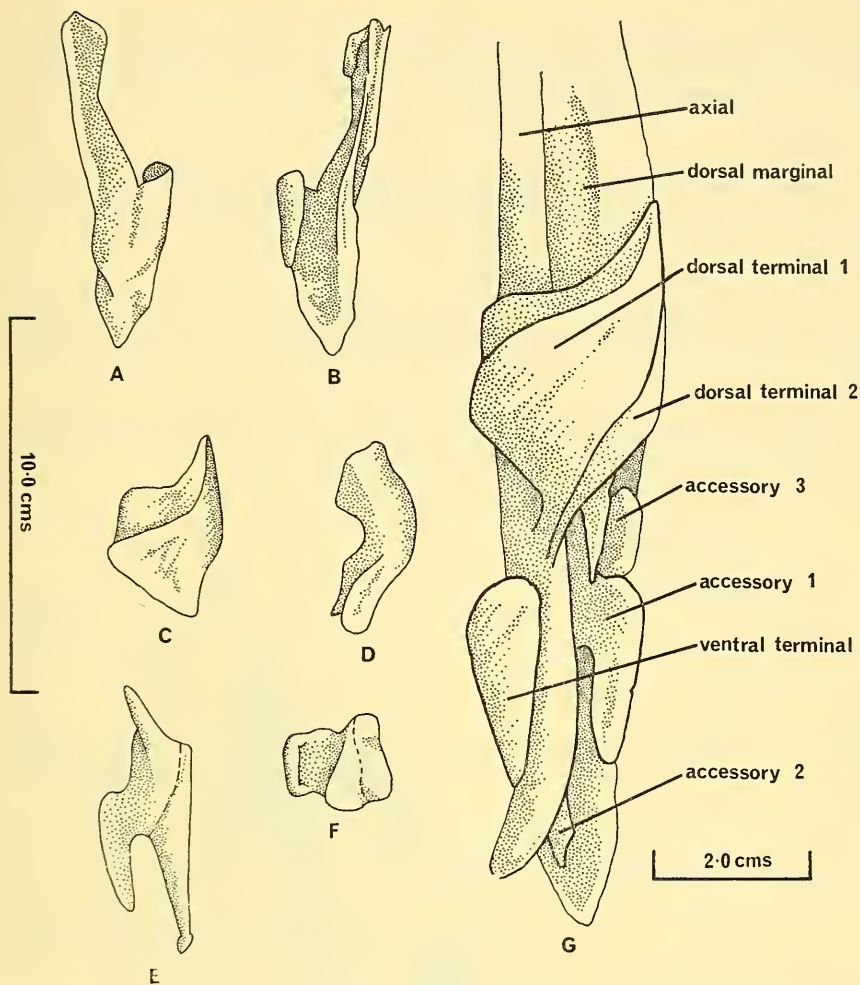


FIG. 3. *Raja rhizacanthus*. Cartilages of the terminal group of the clasper.

A, ventral terminal (ventral view); B, ventral terminal (dorsal view); C, dorsal terminal 1 (dorsal view); D, dorsal terminal 2 (dorsal view); E, accessory cartilages 1 and 2 (dorsal view); F, accessory cartilages 3 and 4 (ventral view); G, terminal cartilages *in situ* from dorsal side.

element, and its knife-edged protruberance is the sentinel. Accessory cartilage 2 is elongate in the longitudinal axis of the clasper, and its distal end is recurved and hook-like, forming the spike of the clasper glans.

5. Accessory cartilages 3 and 4 (fig. 3 F, G)

Accessory cartilages 3 and 4 form the signal of the glans and are situated on the ventral side of the clasper, between the upright portion of the ventral terminal cartilage and the accessories 1 and 2. The smaller proximal cartilage,

accessory 4 is attached in a groove formed between the accessory cartilages 1 and 2 and the ventral marginal cartilage; accessory 3 is movable on accessory 4 and its distal end is bluntly rounded.

Musculature

Only a brief mention of the musculature of *R. rhizacanthus* needs be made for it is identical with that of *R. clavata* as given by Jungersen.

M. dilatator

Proximally this consists of a single muscle mass, but distally it seems to be split into dorsal and ventral muscles. Its origin is on the axial, b_1 and b_2 cartilages, and it inserts as an aponeurosis on the shelf of the dorsal terminal 1 cartilage.

The *m. compressor sacci*, *m. adductor*, *m. flexor* (not *extensor* as given in Jungersen), and muscles of the fin are the same as for *R. clavata*.

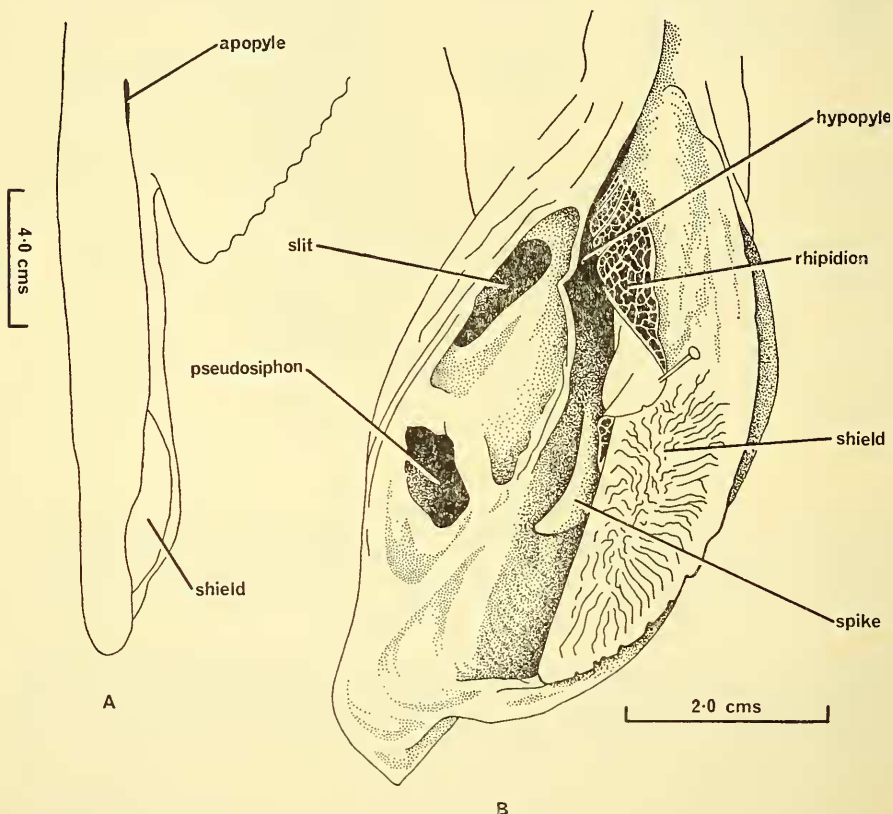


FIG. 4. *Raja pullopunctata*

A, external view of right clasper from dorsal side; B, lateral view of right clasper, opened to show structural features of the glans.

THE CLASPER OF *R. PULLOPUNCTATA* SMITH

The claspers from three adult specimens of *R. pullopunctata*, trawled West of Cape Town and in Algoa Bay were examined.

(i) *The external anatomy of the clasper* (fig. 4 A, B)

The clasper of *R. pullopunctata* is long and stout; its cylindrical body is dorso-ventrally flattened distally, and slightly truncate, giving a spatulate appearance. The glans is much broader than the rest of the clasper, due to the strong development of the shield, which can be clearly seen from the dorsal side. The claspers are entirely naked, scale and spine being absent. The apophyle (fig. 4 A) opens some distance away from the vent, on the dorsal side.

The rhipidion (fig. 4 B) is well developed and fan-shaped and it is attached along the inner ventral wall of the clasper, from the region of the hypophyle to about half-way along the length of the glans. Its lower surface is pitted with cavities of irregular outline, and this spongy tissue is said by Leigh-Sharpe to be erectile and to act as a splash-plate for the ejaculating spermatozoa.

R. pullopunctata may be placed in the pseudogenus *Gamma-raia*, for there is a reduction and crowding of the structural features of the glans. As in all *Gamma-raia*, the signal is absent, while the shield is very well developed and extends along the whole ventral surface of the glans, from the level of the hypophyle almost to the distal extremity of the clasper. The distal region of the shield is covered by pleated epithelia, but this is so thin at the outer lateral edge, that the knife-like appearance of the shield is not unlike the sentinel of *R. rhizacanthus*.

Both the slit and the pseudosiphon are present in the dorsal wall of the concavity of the glans. In *R. pullopunctata* the pseudosiphon is larger and more distally placed than the slit, and these two cavities are separated by a prominent cartilaginous shelf. The pseudosiphon is well separated from the hypophyle by the elongated dorsal marginal cartilage.

Medially placed is a large, single, tongue-like structure, which examination of the terminal cartilages reveals as the spike (cf. Leigh-Sharpe). Although covered by a thick layer of epithelial tissue, the calcified cartilage can be easily felt. The small accessory 1 cartilage is not greatly developed, and the sentinel is not a recognizable element in the external appearance of the clasper.

(ii) *The internal anatomy of the clasper* (fig. 5)

The basipterygium, b_1 and b_2 cartilages and the Beta-cartilage are the same as in *R. rhizacanthus*. The axial cartilage is long, cylindrical at its proximal end, but narrower and dorso-ventrally flattened distally. The distal end of the axial is more heavily calcified than the proximal region, and is slightly curved outwards, terminating in a bluntly rounded point. The dorsal marginal cartilage starts more proximally than the ventral marginal cartilage, and runs for about $2/3$ the length of the axial, to which it is tightly bonded for its entire length. The dorsal marginal cartilage is convex at its proximal end, but becomes

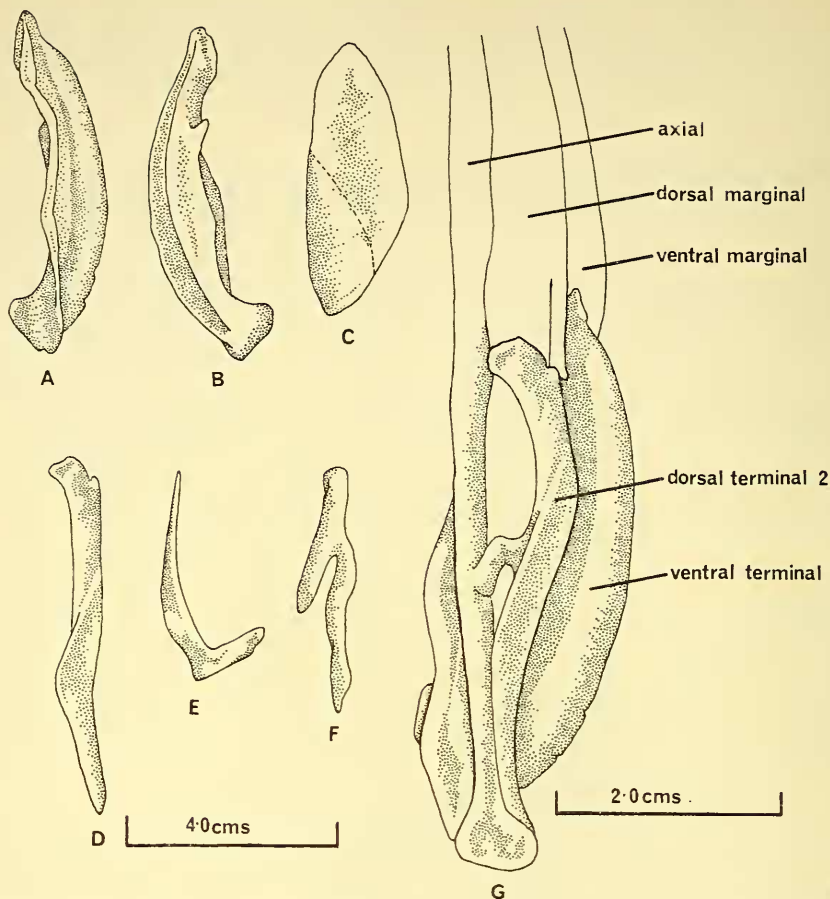


FIG. 5. *Raja pullopunctata*. Cartilages of the terminal group of the clasper.

A, ventral terminal (dorsal view); B, ventral terminal (ventral view); C, dorsal terminal 1 (dorsal view); D, dorsal terminal 2 (dorsal view); E, accessory 1 (ventral view); F, accessory 2 (dorsal view); G, terminal cartilages *in situ* from dorsal side, but with dorsal terminal 1 removed.

flatter distally and is extended in a small point, forming the shelf between the pseudosiphon and the hypopyle. The ventral marginal cartilage is flat and slightly expanded distally, so that it more or less overlaps the axial cartilage, to which it is united. Its distal end is truncate.

1. Ventral terminal cartilage (figs. 5 A, B, G)

As in *R. rhizacanthus*, the ventral terminal is J-shaped, but its distal end is not so strongly developed. The cartilage is attached to the inner surface of the 'scroll-like' ventral marginal cartilage. It is locked to this cartilage by means of

a protuberance, situated ventrally about $\frac{1}{3}$ of the length of the ventral terminal from its proximal end. The protuberance engages with a corresponding point (the minute 'sentinel') of the accessory cartilage 1, hooking the two elements together. The ventral terminal cartilage does not extend to the tip of the clasper. The outer lateral edge of this cartilage is well developed and calcified, forming a convex lamina, the shield of the clasper glans. Distally, the apex of the ventral terminal is grooved, through which the distal regions of the axial and dorsal terminal 2 cartilages pass, before becoming dorso-ventrally flattened. The upright limb of the J-like ventral terminal is raised into a ridge on its dorsal surface.

2. *Dorsal terminal 1* (fig. 5 C)

This cartilage is situated on the dorsal surface of the clasper, and is attached along its outer edge to the dorsal terminal 2 cartilage. The dorsal terminal 1 cartilage is 'shield-like' in appearance and its proximal end is elongated into an obtuse point, to which the dorsal bundle of the *m. dilatator* attaches. The inner distal region of this cartilage is so curved that it wraps around the axial stem and can be seen on the ventral side, where it slightly overlaps the upright limb of the ventral terminal cartilage. Distally, the dorsal terminal 1 is attached by connective tissue to the axial, dorsal terminal 2 and accessory cartilages.

3. *Dorsal terminal 2* (fig. 5 D)

The dorsal terminal 2 cartilage is attached to the inner distal end of the dorsal marginal cartilage, so that the point and connective tissue, which forms the shelf between the pseudosiphon and hypopyle, lie behind the dorsal terminal 1. The dorsal terminal 2 cartilage is a long, thin, single cartilaginous element, curving and then re-curving, so that its pointed distal end is attached to the axial cartilage (fig. 5 G). Proximally, the dorsal terminal 2 is strongly calcified and has a short blunt protuberance on its outer lateral margin, while distally calcification is not so marked, the soft cartilage becoming dorso-ventrally flattened. About half-way along its length, on the inner edge, there is a ligament (forming the shelf between the pseudosiphon and the slit), which arches and inserts on the axial cartilage about $\frac{1}{5}$ the length of this cartilage from its distal end (fig. 5 G).

4. *Accessory cartilage 1* (fig. 5 E)

This minute V-shaped cartilage is attached to the distal end of the ventral marginal cartilage. The longer of its two arms runs forward along the outer lateral edge of the ventral marginal, while the shorter traverses the distal end of the ventral marginal cartilage. The base of the V is slightly pointed (the minute 'sentinel') and is curved inwards, forming the point on which the ventral terminal engages. It must be noted that this cartilage does not manifest itself as an external structural element in the glans.

5. *Accessory cartilage 2* (fig. 5 F)

The accessory cartilage 2 resembles an inverted Y. Its cylindrical proximal end is attached to the inner distal end of the ventral marginal cartilage. The longer limb of the accessory is tightly bonded to the axial, so that distally these two cartilages resemble a single element. The shorter arm of the cartilage is simple in shape and projects laterally outwards. Its terminal end is slightly upturned and forms the spike of the clasper glans.

Musculature

The musculature of *R. pullopunctata* was found to be identical with the description of the musculature of *R. clavata* given by Jungersen, and like *R. batis*, the *m. dilatator* is in two bundles.

(a) *Dorsal m. dilatator*

This muscle has its origin on the proximal region of the axial cartilage and its insertion on the dorsal and lateral regions of the dorsal terminal 1 cartilage. The muscle is not strictly dorsal in position but more medio-dorsal, and is much larger than the ventral *m. dilatator*.

(b) *Ventral m. dilatator*

The muscle is entirely separate from its dorsal counterpart and has its origin on the ventral proximal region of the axial cartilage and the distal end of the b_2 cartilage. It inserts as connective tissue across the surface of the ventral terminal cartilage, although some fibres attach to the tip of the axial cartilage.

The *m. compressor sacci*, *m. adductor*, *m. flexor* and the muscles of the fin are the same as for *R. clavata*.

DISCUSSION

Two pairs of claspers from specimens of *R. batis* Linnaeus, caught S.W. of Ireland, and a pair of claspers from *R. clavata* Linnaeus, caught at Lowestoft, were examined for purposes of comparison.

Although there is a marked difference in the size of the claspers of *R. pullopunctata* and *R. batis*, the general external appearance of the claspers is similar. In both, the clasper is long, stout and naked, becoming dorso-ventrally flattened and spatulate at its terminal end. The outer lateral edge of the shield can be seen from the dorsal side in both species, but in *R. batis* it is more prominent. This may be due to differences in the size of the claspers. However, examination of the clasper glans reveals that the structural features in *R. pullopunctata* and *R. batis* are different (figs. 4 B, 6).

The pseudosiphon and slit are present on the inner dorsal surface of the glans in both species, but their formation is somewhat different, although they are associated with the degree of development of the dorsal terminal cartilages in both cases. In *R. pullopunctata* there is a marked shelf-like ridge separating

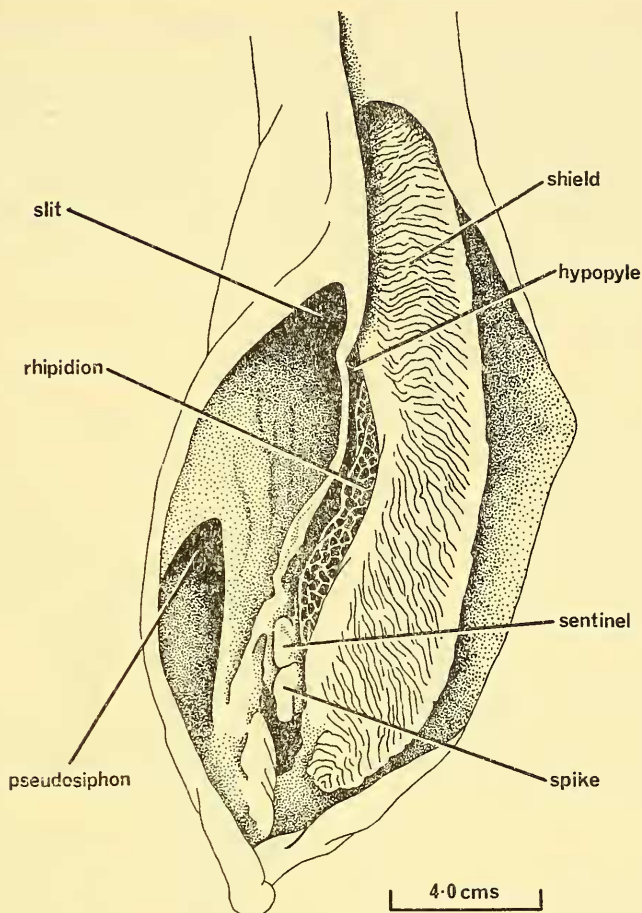


FIG. 6. *Raja batis*. Lateral view of right clasper, opened to show structural features of the glans.

the pseudosiphon from the slit; this shelf is found to be wanting in *R. batis*. The pseudosiphon is similarly situated in the two species, but in *R. pullopunctata* the pseudosiphon resembles a concavity rather than the simple pouch found in *R. batis*. The slit is more proximally situated in *R. pullopunctata*, occurring about half-way along the length of the glans (about one-third the length in *R. batis*). The hypopyle seems to be more distally placed in *R. batis*, but this may be due to the heavier development of the shield. The rhipidion is pitted and fan-shaped in both species, occurring along the inner ventral wall of the hypopyle, and extending about half-way along the length of the glans in *R. pullopunctata* and about two-thirds the length in *R. batis*. The rhipidion is more compact in *R. batis*. The prominent shield extends along the whole inner ventral surface of the glans in both species, but it is thinner and covered with pleated epithelia

along its entire length in *R. batis*, while in *R. pullopunctata* the broader shield is only pleated at its distal region.

The most noticeable difference in the structure of the claspers is in the presence of the enlarged sentinel in *R. batis*, which extends distally and fits together with the spike. In *R. pullopunctata*, the sentinel is reduced and lies under the rhipidion, so that it is not seen when the glans is opened, and these two elements are not expanded terminally as they are in *R. batis*.

As has been pointed out, the visible external characters of the clasper are

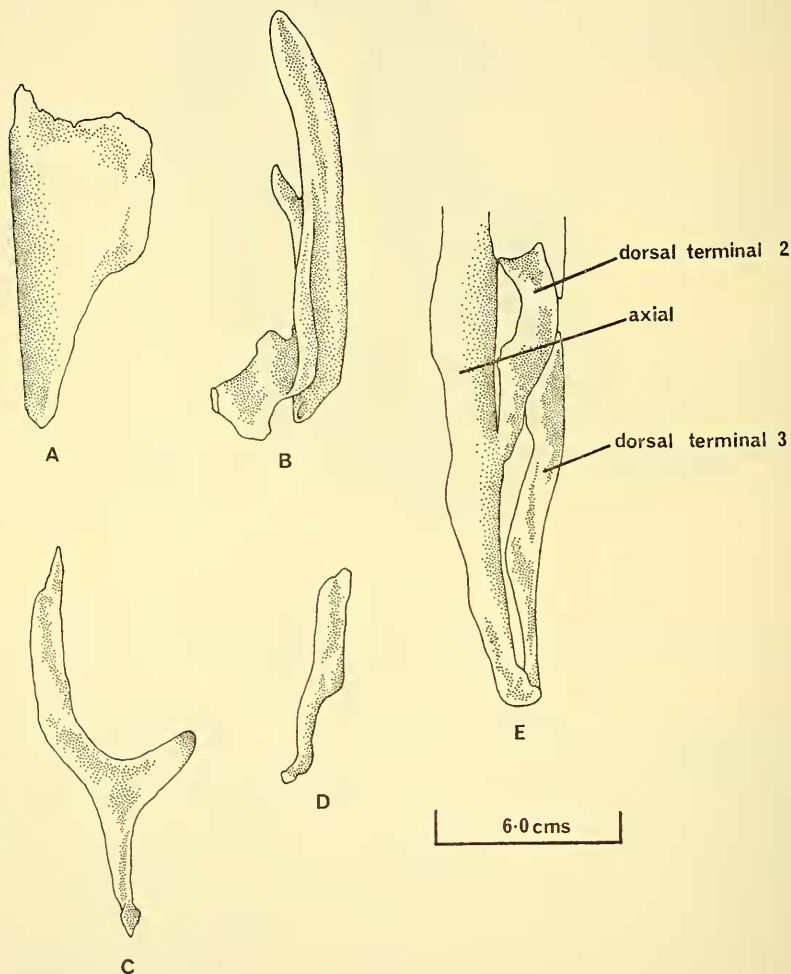


FIG. 7. *Raja batis*. Cartilages of the terminal group.

A, dorsal terminal 1 (dorsal view); B, ventral terminal (dorsal view); C, accessory 1 (dorsal view); D, accessory 2 (dorsal view); E, dorsal terminal 2 and 3 in position.

closely associated with the structure and number of the internal cartilages, and therefore differences in the structure of the glans will be shown by differences in the terminal cartilages. In *R. pullopunctata* there are a total of five cartilages in the terminal group (2 dorsal terminals, 1 ventral terminal and 2 accessory terminals), while in *R. batis* six terminal cartilages are present (3 dorsal terminals, 1 ventral terminal and 2 accessory terminals) (figs. 5, 7).

Although there is a great difference in the size of these elements, their differences in shape and their position may be examined. The dorsal terminal 1 cartilage is similarly situated in both *R. batis* and *R. pullopunctata*, occurring on the dorsal side of the clasper, and it is flat and plate-like, being slightly convex distally. In both species, the median edge is bent in such a manner, that the cartilage wraps round the axial stem and may be seen on the ventral side. Distally, the cartilage is pointed in the two species, but in *R. pullopunctata*, the proximal edge is elongated into a point for the attachment of the aponeurosis of the *m. dilatator*, while in *R. batis* (fig. 7), the proximal edge is almost straight and somewhat more convex. The dorsal terminal 2 cartilage is attached to the distal end of the dorsal marginal cartilage in both species, and it is interesting to note that in *R. pullopunctata*, the dorsal terminal 2 extends to the tip of the axial cartilage, while in *R. batis*, the crescent-shaped dorsal terminal 2 (fig. 7 D, E) is attached to about half way along the axial and that the dorsal terminal 3 extends to the tip of the clasper, i.e. these two cartilages in *R. batis* have been reduced to a single cartilage in *R. pullopunctata*, although there is linking between the dorsal terminal 2 and the axial in both cases. The terminal end of the axial cartilage is similarly curved (laterally outwards) in the two species, and the attachment of the dorsal terminal 2 of *R. pullopunctata* and the dorsal terminal 3 of *R. batis* (fig. 7 E) is similar.

Although both *R. pullopunctata* and *R. batis* possess two accessory cartilages, the accessory cartilage 1 (forming the sentinel) is reduced to a small point in *R. pullopunctata*. In *R. batis* this cartilage (fig. 7 C) is well developed and extends down towards the spike, and fits closely to it. The ventral terminal cartilages are similarly situated in both *R. batis* and *R. pullopunctata* and these elements are similar in shape. Both possess the 'hooking' protuberance on the inner ventral margin, the enlarged convex outer lateral edge and the raised dorsal ridge. However in *R. batis* (fig. 7 B) the distal end of the convex edge projects slightly from the main body of the limb, and the distal end of the ventral terminal is not so markedly grooved as in *R. pullopunctata*.

It may therefore be concluded that, in the structure of the glans and in the number and arrangement of the internal cartilaginous elements, the claspers of *R. pullopunctata* and *R. batis* are different.

Besides differences noted in the structure of the claspers of the two species, some differences can also be seen in the external characters. Smith (1964) points out that there is a difference in shape between the two, but examination of later and adult stages of *R. pullopunctata* reveals that the shape of the disc varies and that the pectorals and anterior margins of the disc become more

concave, as they do in *R. batis*. The author is unable to detect any appreciable difference in shape.

Examination of specimens of comparable size indicates that the inter-orbital is narrower in *R. pullopunctata* than in *R. batis*, and that there is little difference in the comparative size of the eye.

The most noticeable difference is the presence of the large, single, median, nuchal spine in *R. pullopunctata*, which is found both in juveniles and adults (although sometimes worn down). Except about the eyes, the upper surface of the disc is entirely devoid of other large spines, as it is in *R. batis*.

Therefore Smith's proposal that *R. pullopunctata* and *R. batis* are distinct species as based on the general external morphology, is confirmed on the basis of the clasper structure. Recently, two large 'black-bellied' skates, lacking signs of a median nuchal spine, were obtained in trawls off Cape Columbine in 250 fathoms. The external characters of the clasper of the mature male were seen to be identical with those of *R. batis* from European waters. Therefore *R. batis* Linnaeus also may occur off South Africa; however, further investigation on these specimens is necessary.

It is interesting to note that a 'black-bellied' skate from the Falkland Islands, *R. flavirostris* Philippi 1892, greatly resembles the South African *R. pullopunctata* in possessing a single, large, median, nuchal spine. But as yet, clasper material is unavailable for the purposes of comparison.

The author was unable to find a single difference, both in the external structure of the glans and in the number and arrangement of the internal cartilaginous elements, between the claspers of *R. clavata* and *R. rhizacanthus*. The claspers in these two species are identical.

Although Norman points out that the South African species is closely related to the European species, he considers that the two are distinct on the basis of the degree of spination in adults, the position of the vent and the shape of the snout. Preliminary examination of some two hundred specimens of *R. rhizacanthus* has shown that the shape of the snout varies considerably in local populations, as does the degree of spination, and the position of the vent.

Therefore bearing this in mind, and in view of the fact that the claspers are identical, the author agrees with Barnard and Fowler that *R. rhizacanthus* specimens should be referred to *R. clavata* and that *R. rhizacanthus* therefore becomes a synonym of *R. clavata*. This is further supported by the fact that masked bipolarity is already acknowledged in *R. alba*, so that it is not unlikely that distribution of this type also occurs in *R. clavata*.

It may be seen from fig. 8 that the distribution of *R. clavata* ranges from Arctic waters to the tropical waters of the Indian Ocean, having been recorded from greater extremes than *R. alba*. However, through most of their recorded range both species occur in the same waters. As yet, these two species have never been recorded from the equatorial waters of West Africa, but equatorial submergence probably occurs, allowing gene flow from northern hemisphere to southern hemisphere and vice versa.



FIG. 8. Map showing the masked bipolar distribution of *R. alba* and *R. clavata*.

ACKNOWLEDGEMENTS

I am grateful to Messrs. M. J. Holden and C. H. Humphries of the Fisheries Laboratory at Lowestoft for the *R. clavata* and *R. batis* material and to Mr. S. X. Kannemeyer for assistance in collection of the South African skates. My thanks are due to Dr. N. F. Paterson for checking the manuscript and for many helpful recommendations.

The Trustees of the South African Museum acknowledge gratefully the receipt of a grant from the Council for Scientific and Industrial Research towards the cost of publication.

SUMMARY

After detailed studies of the anatomy of the claspers of the males, it is considered that *Raja rhizacanthus* Regan is synonymous with *R. clavata* Linnaeus and that *R. pullopunctata* Smith is distinct from *R. batis* Linnaeus, but that *R. batis* Linnaeus may also occur in South African waters.

REFERENCES

- BARNARD, K. H. 1925. A monograph of the marine fishes of South Africa. *Ann. S. Afr. Mus.* **21**: 1-418.
- BIGELOW, H. B. & SCHROEDER, W. C. 1953. Fishes of the western North Atlantic. Pt. II. Sawfishes, guitarfishes, . . . *Mem. Sears Fdn mar. Res.* **1** (2): 1-588.
- EKMAN, S. 1953. *Zoogeography of the sea*. London: Sidgwick & Jackson.
- FOWLER, H. W. 1936. Marine fishes of West Africa based on the collection of the American Congo Exped. 1909-15. *Bull. Am. Mus. nat. Hist.* **70**: 1-1493.
- FOWLER, H. W. 1940. Fishes of the Philippine Islands and adjacent seas. *Bull. U.S. natn. Mus.* **100**: 1-879.
- FRANCA, P. DA. 1959. Subsídio para um catálogo dos nomes vernáculos dos peixes marinhos de Angola. *Notas mimeogr. Cent. Biol. pisc.* **5**: 1-37.
- FRIEDMAN, M. H. F. 1935. The function of the claspers and clasper glands in the skate. *J. biol. Bd. Can.* **1**: 261-268.
- HUBER, O. 1901. Die Kopulationsgleider der Selachier. *Z. wiss. Zool.* **70**: 592-674.
- ISHIYAMA, R. 1958. Studies on the rajid fishes (Rajidae) found in the waters around Japan. *J. Shimonoseki Coll. Fish.* **7**: 193-394.
- JUNGENSEN, H. F. E. 1899. On the Appendices genitales in the Greenland shark *Somniosus microcephalus* and other selachians. *Dan. Ingolf-Exped.* **2** (2): 1-88.
- LEIGH-SHARPE, W. H. 1920. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Mem. I. The claspers, clasper siphons and clasper glands. *J. Morph.* **34**: 254-265.
- LEIGH-SHARPE, W. H. 1921. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Mem. II. *J. Morph.* **35**: 263-358.
- LEIGH-SHARPE, W. H. 1922. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Mem. III, IV, V. *J. Morph.* **36**: 191-244.
- LEIGH-SHARPE, W. H. 1924. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Mem. VI, VII. *J. Morph.* **39**: 553-577.
- LEIGH-SHARPE, W. H. 1926. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Mem. VIII, IX, X, XI. *J. Morph.* **42**: 307-368.
- MAYR, E., LINSLEY, E. G. & USINGER, R. L. 1953. *Methods and principles of systematic zoology*. New York: McGraw-Hill.
- NORMAN, J. R. 1935. Coast fishes Pt. I. The South Atlantic. 'Discovery' Rep. **12**: 3-58.
- PIETSCHMANN, V. 1906. Ichthyol. ergebnisse einer reise nach Island. *Annln. naturh. Mus. Wien.* **21**: 72-148.
- PETRI, K. R. 1878. Die Copulations-organe der Plagiostomen. *Z. wiss. Zool.* **30**: 288-335.
- SMITH, J. L. B. 1961. *The sea fishes of southern Africa*. Cape Town: C.N.A.
- SMITH, J. L. B. 1964. Fishes collected by Dr. Th. Mortenson off the coast of South Africa in 1929, with an account of the genus *Cruriraja* in South Africa. *Vidensk. Meddr dansk naturh. Foren.* **126**: 283-300.
- WHITE, E. G. 1937. Interrelationships of the elasmobranchs with a key to the order Galea. *Bull. Am. Mus. nat. Hist.* **74**: 87-117.